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Soil moisture and its importance for tundra plants

JULIA KEMPPINEN



UNIVERSITY OF HELSINKI
FACULTY OF SCIENCE

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JULIA KEMPPINEN

ACADEMIC DISSERTATION

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|---------------|--|
| Author | Julia Kemppinen Department of Geosciences and Geography University of Helsinki, Finland |
| Supervisor | Miska Luoto Department of Geosciences and Geography University of Helsinki, Finland |
| Opponent | Signe Normand Department of Biology Aarhus University, Denmark |
| Pre-examiners | Bente Graae Department of Biology Norwegian University of Science and Technology, Norway Aimée Classen Rubenstein School of Environment and Natural Resources University of Vermont, United States of America |
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Abstract

Water is fundamental for plant life, as it affects the growth, survival, and spatial patterns of vegetation. Here, I explored soil moisture and its ecosystem effects to answer: 1) What controls soil moisture variation? 2) How is water linked to vegetation? 3) Do plants influence water resources? I focused on the moisture of the top-soil layer (0–10 cm) in Fennoscandian mountain tundra.

First, I evaluated environmental conditions controlling soil moisture variation. I used different modelling methods (generalized linear models, generalized additive models, generalized boosted regression models, and random forests) to account for the uncertainties related to each multivariate technique. On average, the model fit was $R^2 = 0.60$ and the predictive performance $R^2 = 0.47$. The spatial variation of soil moisture was most related to a topographic proxy of soil water accumulation and the depth of the organic soil layer. These results demonstrated that moisture can be modelled using topography and soil data.

Secondly, I examined the influence of three water aspects (spatial and temporal variation of soil moisture, and fluvial disturbance) on vascular plants, mosses, and lichens. I used species distribution modelling, a framework for analysing the spatial patterns of species in relation to the environment. The species groups were most related to the spatial variation of soil moisture, albeit species had diverse responses. In general, water is not scarce in the tundra, yet the water aspects improved the models highlighting water as a multifaceted driver of the ecosystem.

In addition, I investigated if plant-environment relationships were universal in the tundra. Here, I used hierarchical generalized additive models to compare sites across the hemispheres. I combined plant trait records with data on their environmental drivers. The local variation of conditions within the sites was overridden by global relationships indicating that these links are generalisable across the tundra sites. The results provide empirical evidence for a fundamental assumption in community ecology: consistent plant-environment relationships.

Last, I introduced plants to my first question regarding controls of soil moisture. I considered other factors potentially influencing vegetation and soil conditions by using structural equation modelling, a theory-based hierarchical modelling technique. Woody plants correlated negatively with soil moisture, soil temperature, and soil organic carbon stocks (standardised coefficients = -0.16; -0.22; -0.27). As the abundance of woody plants increases, they feedback into the climate system through the water, energy, and carbon cycles.

To conclude, plant-water relationships are strong across the tundra. Soil moisture and its spatial variation are controlled by the soil characteristics and the topographic features in the landscape, but also by the abundance of woody plants. Water conditions affect vegetation across species groups, from individuals to the communities. This knowledge unravels the importance of soil moisture in a vulnerable ecosystem undergoing rapid changes.

Abstract in Finnish

Vesi on välttämätöntä elämälle, myös kasveille. Vesi vaikuttaa kasvillisuuden kasvuun, eloonjääntiin ja alueelliseen esiintyvyyteen. Tässä väitöskirjassa tutkin maaperän kosteutta ja sen vaikutuksia paljakkaekosysteemiin vastaamalla seuraaviin kysymyksiin: 1) Mikä vaikuttaa maaperän kosteuden vaihteluun? 2) Kuinka vesi kytkeytyy kasvillisuuteen? 3) Vaikuttavatko kasvit vesiresursseihin? Tutkimuksissani tarkastelin pintamaan (0 – 10 cm) kosteutta Fennoskandian tunturipaljakalla.

Väitöskirjani ensimmäisessä osassa tutkin kosteuden säätelijöitä. Käytin useita tilastollisia mallinnusmenetelmiä (yleistä lineaarista mallia, yleistä additiivista mallia, yleistettyä luokittelupuu menetelmää ja satumetsää), sillä kaikissa on omat epävarmuustekijänsä. Keskimäärin mallin istuvuus oli $R^2 = 0.60$ ja ennustuskky $R^2 = 0.47$. Kosteuden alueellista vaihtelua sääteli eniten pinnanmuotoihin perustuva kosteusindeksi ja turpeen paksuus. Tulokset osoittavat, että kosteutta voi mallintaa topografia- ja maaperäaineistolla.

Toisessa osassa tarkastelin kolmea vesimuuttujaa (kosteuden alueellista ja ajallista vaihtelua sekä veden aiheuttamia häiriöitä) ja niiden vaikutusta putkilokasveihin, sammaleisiin ja jäkäliin. Käytin lajimallinnusta, joka on kehitetty lajien ja niitä säätelevien tekijöiden alueelliseen tarkasteluun. Kolmesta vesimuuttujasta kaikkia lajiryhmä sääteli eniten kosteuden alueellinen vaihtelu. Vesimuuttujat paransivat malleja, mikä osoittaa, että vesi vaikuttaa suuresti paljakkaekosysteemissä, missä vedestä ei yleensä ole pulaa.

Lisäksi tutkin kasvien ja ympäristön välistä suhdetta ja sen yleistettävyyttä paljakalla. Käytin hierarkkista yleistä additiivista mallia vertaillakseni alueita kummaltakin pallonpuoliskoilta. Tarkastelin kasvien toiminnallisten ominaisuuksien säätelijöitä. Paikallista ympäristövaihtelua merkittävämpää oli kasvien ja ympäristön johdonmukainen suhde. Tulokset osoittavat todeksi yhden toiminnallisen ekologian tärkeimmistä olettamuksista: kasvien ja ympäristön suhde on yleismaailmallinen.

Viimeisessä osassa palasin ensimmäiseen kysymykseeni kasvien kera. Käytin rakenneyhtälömallia, joka on teoriaperusteinen hierarkkinen menetelmä ja mahdollistaa taustamuuttujien huomioimisen. Puuvartinen kasvillisuus korreloi negatiivisesti maaperän kosteuden, maaperän lämpötilan ja maaperän eloperäisen hiilivaraston kanssa (standardoidut kertoimet = -0.16; -0.22; -0.27). Kun paljakka ympäristö pensastuu, puuvartinen kasvillisuus tulee vaikuttamaan ilmastoon veden, energian ja hiilen kierron kautta.

Johtopäätökseni on, että kasvien ja veden välinen vuorovaikutussuhde on voimakas paljakalla. Maaperän kosteus ja sen alueellinen vaihtelu on maaperän ja pinnanmuotojen säätlemää, mutta myös puuvartinen kasvillisuus säätelee sitä. Vesiolot vaikuttavat kasvillisuuden eri lajiryhmiin, niin yksilöihin kuin yhteisöihin. Tämä tieto korostaa kosteuden merkitystä herkässä ekosysteemissä, jota koettelevat suuret muuttokset.

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“Time flies, start reading now”, he said to a lecture hall full of first year geography students in September 2011. This advice was the first of many I have since gotten from my supervisor. Thank you Miska Luoto for the advice, the opportunities and these years. I must also thank Peter C. le Roux and Juha Aalto for their encouragement, as well as Heidi Mod and Annina Niskanen for inspiring me to pursue a PhD.

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Finally, my partner in crime, Pekka Niittynen, thank you for literally carrying me across the mental, emotional and physical topographies of life.

In Helsinki, Finland, April 16th 2020,

Julia Kemppinen

PS Special thanks to Jo Harding in *Twister* (Universal Pictures 1996), what an inspiration for a young woman in science!

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| Articles I, II, III & IV | | | |

| Article | | | Abbreviation | Meaning | Category |
|----------|------------|----------------------|--------------|---|-----------|
| I | II | IV | GAM | Generalized additive model | Methods |
| I | II | | GBM | Generalized boosted regression model | Methods |
| I | II | | GLM | Generalized linear model | Methods |
| | | IV | HGAM | Hierarchical generalized additive model | Methods |
| I | III | | LiDAR | Light detection and ranging | Materials |
| | II | | NMDS | Non-metric multidimensional scaling | Methods |
| | | IV | PCA | Principal component analysis | Methods |
| I | II | | RF | Random forest | Methods |
| | II | | SDM | Species distribution model | Methods |
| | III | | SEM | Structural equation model | Methods |
| I | III | | TPI | Topographic position index | Materials |
| I | III | | TWI | Topographic wetness index | Materials |
| I | II | III IV | VWC | Volumetric water content | Materials |

Articles and contributions

This thesis is based on the following articles referred by the Roman numeral.

- I** Julia Kemppinen, Pekka Niittynen, Henri Riihimäki & Miska Luoto (2018). Modelling soil moisture in a high-latitude landscape using LiDAR and soil data. *Earth Surface Processes and Landforms*. DOI: 10.1002/esp.4301
- II** Julia Kemppinen, Pekka Niittynen, Juha Aalto, Peter C. le Roux & Miska Luoto (2019). Water as a resource, stress and disturbance shaping tundra vegetation. *Oikos*. DOI: 10.1111/oik.05764
- III** Julia Kemppinen, Pekka Niittynen, Anna-Maria Virkkala, Konsta Happonen, Henri Riihimäki, Juha Aalto & Miska Luoto (*Under review*). The influence of woody plants on tundra soils. Preprint DOI: 10.1101/789743
- IV** Julia Kemppinen, Pekka Niittynen, Peter C. le Roux, Mia Momberg, Konsta Happonen, Juha Aalto, Helena Rautakoski, Brian J. Enquist, Vigdis Vandvik, Aud H. Halbritter, Brian Maitner & Miska Luoto (*Under review*). Consistent plant trait-environment relationships within and across tundra communities.

| Article | Idea | Data | Analysis | Writing |
|---------|------------|----------------------------|------------|--|
| I | JK, ML | JK, PN, HR | JK, PN | JK, PN, HR, ML |
| II | JK, PN, ML | JK, PN, JA, PR, ML | JK, PN | JK, PN, JA, PR, ML |
| III | JK | JK, PN, A-MV, HR | JK, KH | JK, PN, A-MV, KH, HR, JA, ML |
| IV | JK, ML | JK, PK, PR, MM, JA, HR, ML | JK, KH, BE | JK, PK, PR, MM, KH, JA, HR, BE, VV, AH, BM, ML |

1 Introduction

Water is pivotal for life on planet Earth. In climate change impact studies, the importance of water is often underestimated in tundra environments (le Roux *et al.* 2013). Nevertheless, climate change will significantly affect the hydrosphere and cryosphere of these systems (Fountain *et al.* 2012, Bring *et al.* 2016). As temperature, precipitation, ice, snow, permafrost, and the overall hydrological conditions are changing in the tundra, plant-available water is also likely to change (Barnett *et al.* 2005, Blankinship *et al.* 2014). Thus, in a warmer future, plant-water relationships will be more important than ever (McLaughlin *et al.* 2017, Robinson *et al.* 2019).

Knowledge on soil moisture and its spatial and temporal variation is crucial for ecosystem research. Water affects the growth, survival, and spatial patterns of vegetation (Whittaker 1972, Franklin *et al.* 2016). Yet, in the tundra, the influence of fine-scale distribution of moisture on terrestrial vegetation characteristics is a pronounced research gap in ecology (Hodkinson *et al.* 1999, Crimmins *et al.* 2011, Silvertown *et al.* 2015, McLaughlin *et al.* 2017).

1.1 Objectives

A major motivation for this thesis is global environmental change (Seddon *et al.* 2016), which is particularly rapid (Post *et al.* 2019) and strongly connected to soil moisture across the tundra regions (Winkler *et al.* 2016, Robinson *et al.* 2018, Saros *et al.* 2019). Here, plant-water relationships must be thoroughly investigated. Tundra ecosystems also provide an ideal environment for testing ecological hypotheses and exploring complicated questions (French and Smith 1985). It is a rather simple ecosystem with relatively few species and due to its remoteness, human impact on soil, water, and plants is low.

In the tundra, important issues regarding plant-water relationships calls for investigation. Firstly, the fine-scale spatial variation of soil moisture influenced by the landscape factors are rarely quantified (Robinson *et al.* 2008, Korres *et al.* 2015). Secondly, the role of plant-available water shaping the spatial distributions and functional traits of tundra plants requires evaluation (Crimmins *et al.* 2011, le Roux *et al.* 2013, Bjorkman *et al.* 2018a). Lastly, the significant impact of plants on water resources must be addressed in examining plant-water relationships (Aalto *et al.* 2013, Robinson *et al.* 2019).

Here, I dig deep into the complex plant-water relationships to provide insights to urgent scientific concerns. I explored surface soil moisture (< 10 cm) and its importance for tundra plants as I sought answers to my questions (Table 1).

1.2 Soil moisture

Soils are the interface on the life-sustaining critical zone (Lin 2010, Banwart 2011, Kirkby 2016). Soil moisture is an important storage of water and a key component of the hydrological cycle (Figure 1) (Western *et al.* 2002, Legates *et al.* 2011), although this liquid or frozen water stored in soils constitutes a minor proportion of all water (Shiklomanov 1993). Soil moisture is affected by water fluxes between the soils, biota, and climate that influence, for instance, surface runoff, transpiration, and precipitation (Figure 1) (Huggett *et al.* 2002). In addition, terrain ruggedness and other landscape characteristics play a major role in controlling the hydrological cycle of the ecosystem, particularly in mountain tundra.

Soil moisture is an integrative and unifying

theme in physical geography, as it is in the intersection of climatology, hydrology, geomorphology, and biogeography (Figure 1) (Legates *et al.* 2011). It influences land-atmosphere fluxes, runoff generation, landscape denudation, and the establishment of vegetation. In turn, the abiotic and biotic factors also shape the spatial and temporal variation of soil moisture through example evaporation, precipitation, drainage, and transpiration (Figure 1).

Soil moisture may vary across scales (Figure 2) (Engstrom *et al.* 2005, Seneviratne *et al.* 2010, Korres *et al.* 2015), due to factors of multiple scales controlling the lateral and vertical movement of water in soils (Robinson *et al.* 2008). Planetary scale factors determine global and continental precipitation and evaporation, whereas at the fine scale, local factors are more significant for soil moisture (Grayson *et al.* 1997, Wilson and Gallant 2000, Korres *et al.* 2015).

For instance, local distribution of soil water is influenced by the physical soil characteristics, terrain ruggedness, and the overlaying vegetation (Crave and GascuelOdoux 1997, Western *et al.* 2002).

Essentially, there are two ways to obtain soil moisture data: ground-based point-measurements and remotely-sensed satellite observations. The first represents a fine-scale approach, with the high support of circa 1 dm³ (depending on the measurement device) and has the possibility for frequent spacing, but a relatively limited spatial extent (Robinson *et al.* 2008) (Figure 3). The latter is at a broader scale, as its spatial extent may cover the entire land surface of the Earth, but it has a low support (Figure 3). However, there is a knowledge gap regarding the intermediate scale, representing, for instance, small watersheds, such as catchments and sub-watersheds (Crave and GascuelOdoux 1997, Robinson *et al.* 2008).

Field measured soil moisture can be

Table 1. Hypotheses. The data and model structures are described in Table 2 and Table 3.

| Question | Article | Aims and hypotheses |
|---|---------|---|
| 1. What controls soil moisture variation? | I | To quantify both spatial and temporal variation of fine-scale soil moisture across a high-latitude landscape, as I hypothesised that the soil and topography properties would influence the moisture patterns and they would increase the predictive performance of the models. |
| 2. How is water linked to vegetation? | II | To study how multiple water aspects influence fine-scale species distributions, species richness and community composition in the tundra, as I hypothesised that water would have a significant role in shaping assemblages of vascular plants, mosses and lichens in tundra. |
| | III | To assess if there are consistent plant-environment relationships within and across tundra ecosystems for testing a fundamental hypothesis in community ecology: relationships between plants and environmental conditions are globally consistent. |
| 3. Do plants influence water resources? | IV | To investigate if woody plants affect fine-scale soil properties in the tundra, while controlling for other influencing factors, as I hypothesised that woody plants would have direct effects on soil moisture, soil temperature, and soil organic carbon stocks. |

determined as a volumetric value, meaning that the volume of water is divided by the volume of the soil (Western *et al.* 2002). It is also important to define the soil depth that the value represents, as for instance, in the upper soil layers (< 50 cm depth), water is more affected by plant-atmosphere fluxes compared to deeper soil layers. Soil moisture varies over space and time, as it is affected by processes of different scales (Western *et al.* 2002). These scale effects must be carefully considered from the extent, spacing, and support perspectives (Figure 3).

Field-quantified, intensively spaced, and spatially extensive soil moisture data are expensive and time-consuming to collect (Famiglietti *et al.* 2008, Hájek *et al.* 2013, Wild *et al.* 2019). Consequently, it is difficult to measure comprehensively *in situ* soil moisture at the fine scale on large extents (Robinson *et al.* 2008). For this reason, topography-based proxies are often used instead (Kopecký and Čížková 2010). Proxies are based on the physical characteristics of landscape features, as topography influences the flow of the surface and subsurface water

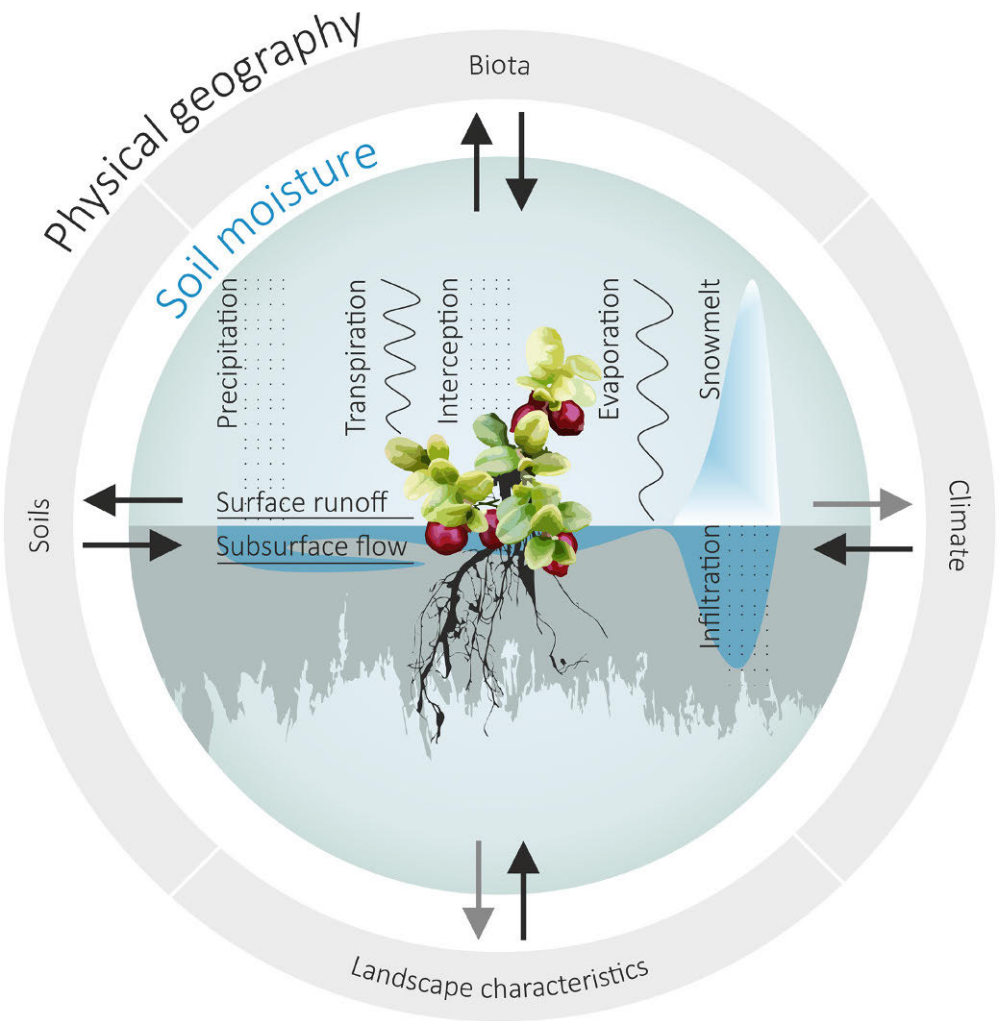


Figure 1. Soil moisture in the field of physical geography. Multiple water fluxes affect soil moisture (in blue), even when lateral flow (Figure 4) is minimal. Dark arrows represent strong links. Modified from Western *et al.* (2002) and Legates *et al.* (2011).

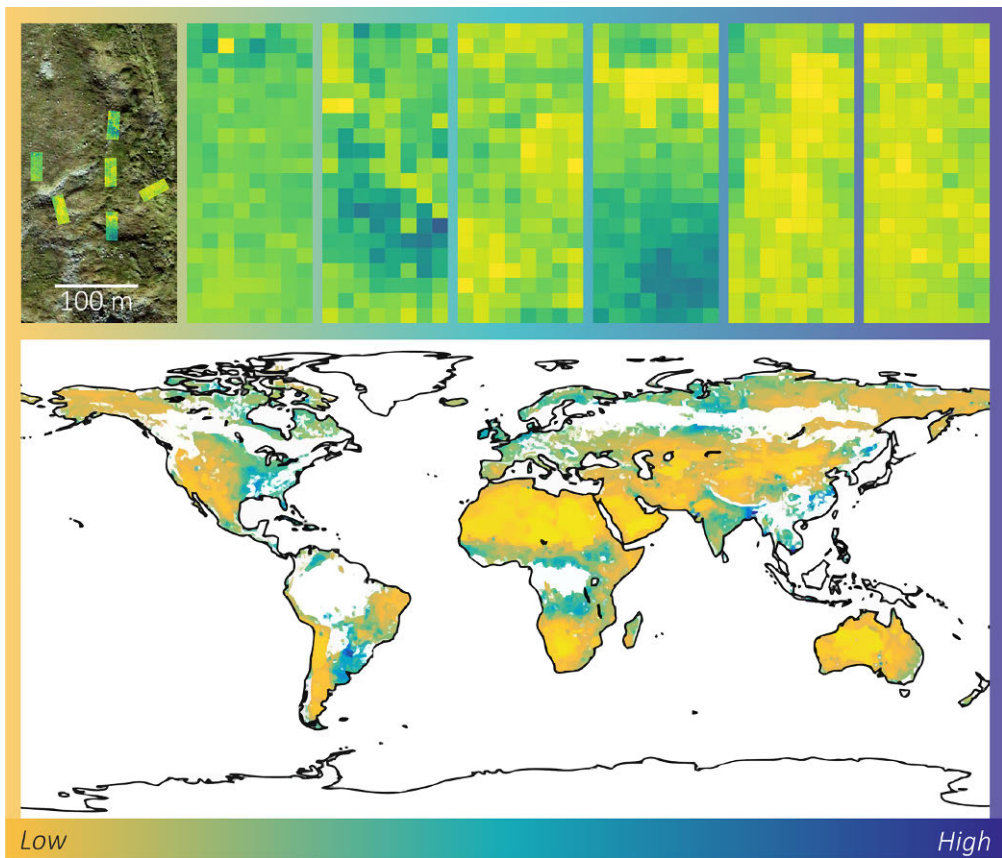


Figure 2. Spatial distribution of soil moisture. The top row represents field-measured soil moisture variation at the fine-scale. Each pixel represents 1 m² and the six grids are located < 200 m apart. The global map shows the remotely sensed distribution of soil moisture with a 40 km spatial resolution. White regions on land are missing data. Modified from le Roux *et al.* (2013), McColl *et al.* (2017), **Article II.**

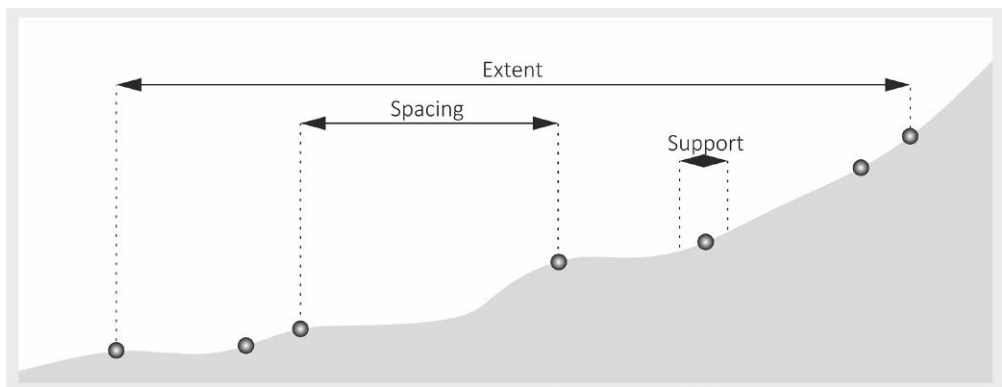


Figure 3. The scale of soil moisture. The extent refers to the overall spatial or temporal coverage of the values. As spacing decreases in time or space, the amount of details increases. Support describes the area or time, over which homogenous conditions are assumed. In other words, it expresses the coverage or volume, which a given soil moisture measurement represents. The dots represent individual measurements in space or time. Modified from Western *et al.* (2002), Kempainen (2016).

(Beven and Kirkby 1979).

In complex topography, the slope angle and upslope ground-surface conditions can vary from one meter to another, which is reflected on the spatial distribution of surface water flow (Figure 2) (Isard 1986, Crave and GascuelOdoux 1997). This means that slope variation is reflected in the availability of moisture in shallow soils in hilly landscapes (Figure 4) (Hoylman *et al.* 2018). Thus, topographic wetness indices provide a relatively realistic and accessible model of the general patterns of surface moisture and its spatial distribution (Beven and Kirkby 1979, Kopecký and Čížková 2010).

In addition to topography, also soil physical characteristics influence moisture conditions (Darmody *et al.* 2004). Soil structure and texture affects the water-holding capacity of the

soil and, in turn, controls water infiltration and percolation (Cosby *et al.* 1984, Teuling and Troch 2005, Fatichi *et al.* 2020). For instance, organic soils can store water relatively well (Figure 4) (Darmody *et al.* 2004, Legates *et al.* 2011), whereas impeding layers in the soil profile direct the drainage within the soil. Drainage of moisture through the soil layers is the main source of groundwater recharge (Western *et al.* 2002).

Besides abiotic conditions, plants also play an important role in soils through their biophysical and biochemical properties (Loranty *et al.* 2011, Parker *et al.* 2015, Seaton *et al.* 2019). For instance, plants influence the above- and below-ground soil processes (Figure 4), such as decomposition (Cahoon *et al.* 2012), evapotranspiration (Robinson *et al.* 2008), soil water repellency (Seaton *et al.* 2019), and soil

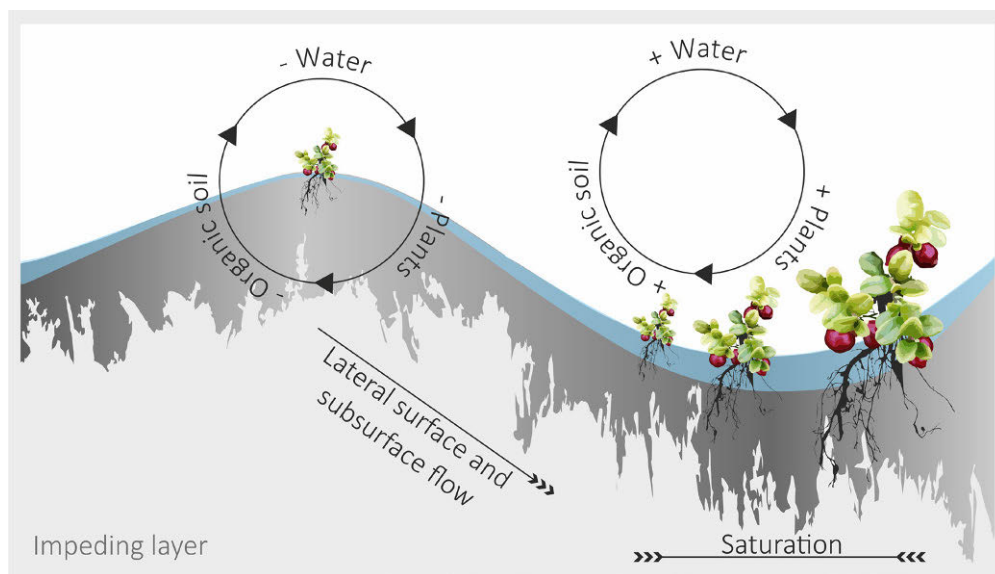


Figure 4. Topography and soil properties on soil moisture. In addition to the water fluxes (Figure 1), lateral flow has a significant control on the spatial distribution of soil moisture in varying topography. In the higher parts of the relief, such as ridges and hilltops, more water (blue) is depleted due to lateral flow and drainage. This channels water into the lower parts of the relief, such as depressions, leading to saturation and formation of organic soils, if water and plant material accumulates on top of the impeding layer. Organic soils (in dark grey) can store larger amounts of water compared to mineral soils (light grey). In water-accumulating depressions, saturation creates anoxic conditions, where plant roots absorb oxygen poorly from the soil. Whereas, on well-drained ridges and slopes, plants are exposed to drier soils due to drying winds, higher evaporation, and soils that contain less organic material, and in turn, less moisture. Gradients in elevation and aspect affect the amount of water and energy that is available for plants. Overall, topographic complexity increases variability in the spatial distribution of soil moisture (Crave and GascuelOdoux 1997) and, in turn, decreases ecosystem sensitivity to climatic changes (Hoylman *et al.* 2018). Modified from Billings (1973), Western *et al.* (2002), (Kempainen 2016).

formation (Billings 1973).

Plants transpire water. Transpiration can lead to significant decreases in soil water storages during increased temperatures (Mastrotheodoros *et al.* 2020). In the tundra, plants also shade soils, which decreases soil temperatures, and in turn, decreases evaporation (Humphreys 1907, Graham *et al.* 2012, Aalto *et al.* 2013). In addition, vegetation may also influence the availability of soil moisture through rainfall interception and increase drainage in the root zone as their roots dig macropores into the soil (Western *et al.* 2002, Bonfils *et al.* 2012, Zwieback *et al.* 2019). Thus, this ecohydrological aspect of plant influence must be accounted for in soil moisture investigations (Porporato and Rodriguez-Iturbe 2002, Robinson *et al.* 2019, Mastrotheodoros *et al.* 2020).

1.3 Tundra

The tundra biome is characterised by its short growing season, which is due to the macroclimatic conditions of the Arctic, Antarctic and alpine realms (Strahler and Strahler 2005) (Figure 5). Towards the winter of the high-latitudes, days get short, dark, cold, and snowy as solar elevation decreases and, in turn, night length increases (Sakai and Larcher 2012). Contrastingly in summer, the days are long and nights very short or even absent. Consequently, the daytime temperatures rise above 0°C degrees, the soil surface thaws, and plants can grow during this brief period of abundant resources: light, nutrients, and water found in its liquid phase (Sonesson and Callaghan 1991).

Tundra plants and landscapes are influenced by frost and snow (Billings and Mooney 1968, Sakai and Larcher 2012). Seasonality controls the plant-available resources and plant-affecting disturbances. Most of the plant-available water is found in the topsoil layers supplied by precipitation, groundwater, melting snow patches, and thawing

permafrost (Barichivich *et al.* 2014, Blankinship *et al.* 2014, Bring *et al.* 2016). In winter, moisture freezes and forms ground frost, needle ice, and frost-heaving (French 2007), which damages plants as roots are exposed and uprooted (Sakai and Larcher 2012).

In spring, snow provides an abundance of meltwater streams, which cause fluvial disturbance that affects vegetation as water erodes and accumulates sediments on the ground surface (Giblin *et al.* 1991). Although meltwater is a disturbance, it also provides moisture, but when surface flow is excessive, waterflow may rip small sessile organisms from the soil or cover them under sediments (Giblin *et al.* 1991). On the other hand, this type of disturbance may also have positive effects, for instance, on specialist alpine vascular plants species, as they compete with boreal species for resources (le Roux *et al.* 2014).

Towards the end of the growing-season, melting snow patches provide moisture as the landscape dries (Barichivich *et al.* 2014, Winkler *et al.* 2016). However, earlier melting interrupts the recharge of this vital resource (Blankinship *et al.* 2014). This may lead to drying later in summer and forces plants under water-stress (Bintanja and Andry 2017, Kankaanpää *et al.* 2018).

In the tundra, soil moisture and soil temperature have a significant negative correlation during the growing-season (Aalto *et al.* 2013). Soil moisture-temperature relationship is crucial for the above- and below-ground ecosystem functions (Classen *et al.* 2015). From an abiotic perspective, a slight increase in soil moisture can buffer against enhanced freeze-thaw cycling of the top-layer of permafrost (Wlostowski *et al.* 2018). This negative relationship with soil temperature also promotes the establishment of habitats in favourable microclimatic conditions, which are referred to as refugias (Ashcroft and Gollan 2013).

This means that fine-scale variation of moisture creates microclimatic pockets or microhabitats, that is, the environmental conditions, which may shift over short distances (McLaughlin *et al.* 2017). This is reflected on the distribution of tundra plant communities creating mosaic-like patterns in the landscape (Billings 1973).

Polar tundra across the hemispheres share numerous similarities despite their floristic differences, that is, unique species pools (French and Smith 1985). In general, plants are relatively

low in stature and long-living, and the main groups consist shrubs, dwarf shrubs, graminoids, herbs, mosses, and lichens.

On the global scale, tundra vascular plants have relatively shallow roots (Canadell *et al.* 1996). However, they store most of their biomass below the soil surface, as only 10-50% of their biomass is located above-ground (Iversen *et al.* 2015). Besides vascular plants of the tundra, the less studied species groups, mosses and lichens, are also affected by the spatial variation of soil moisture in multiple ways, although they are

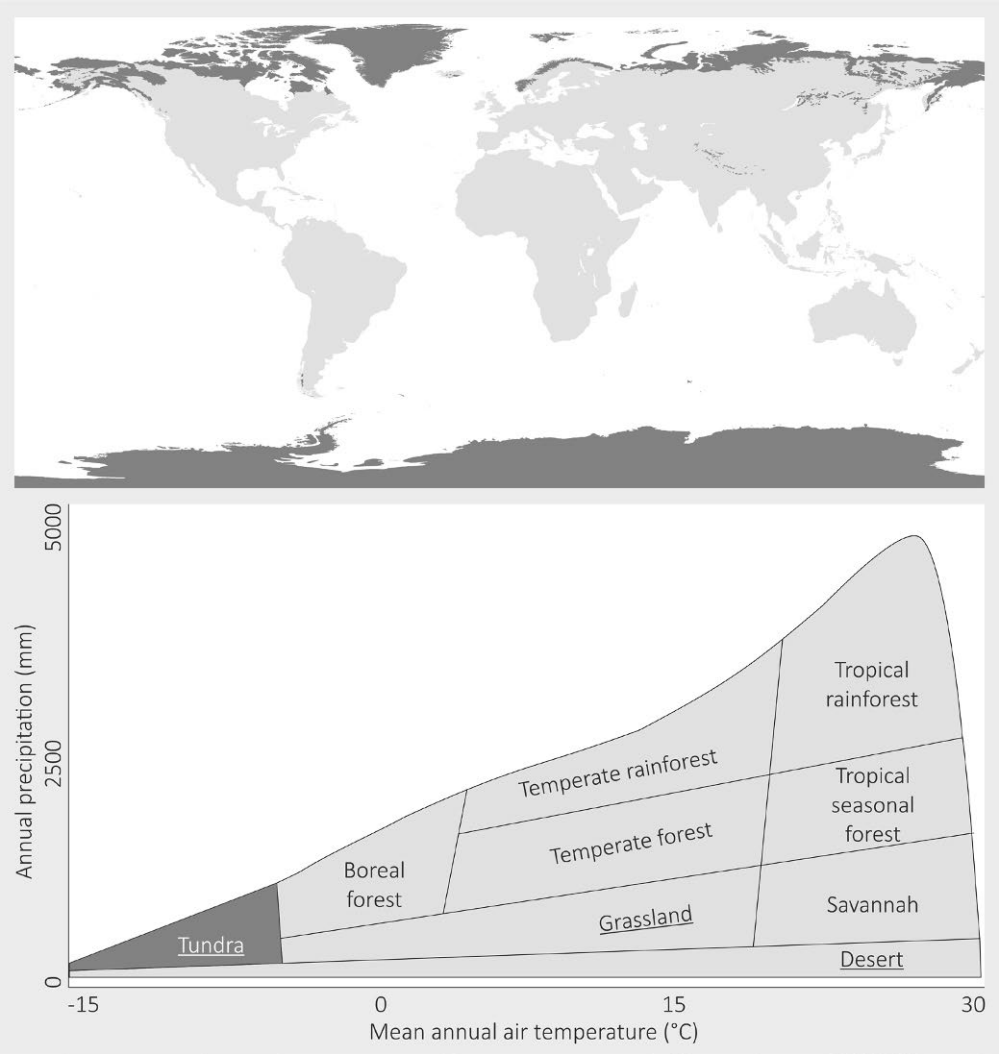


Figure 5. The tundra in geographical and environmental space. The treeless biomes are underlined. Modified from Whittaker (1970), Woodward and Lomas (2004), Dinerstein *et al.* (2017).

not as dependent on the water resources of the deeper soil layers (Iturrate-Garcia *et al.* 2016, Kern *et al.* 2019). For instance, mosses and lichens lack a root system and therefore, suffer less of mechanical disturbance, such as freezing and thawing of the soil (Jonasson 1986). Often, mosses also dominate in water-logged habitats, in conditions where vascular plants may suffer of anoxia. All in all, these three species groups are the cornerstones of the tundra ecosystem, as they are largely responsible for the primary production and biomass (Bjerke *et al.* 2011).

Soils can be divided into mineral and organic, depending on the amount of biological material in them (Strahler and Strahler 2005). The first is formed, when rock cracks into aggregates, pieces of soil material. Large aggregates form well drained soils, as between the particles remain gaps occupied by, for instances, water, air, and plant roots (Huggett *et al.* 2002). Organic soils are produced by microorganisms, which decompose dead material, such as plant litter. In low temperatures, soil microbial activity decreases, and decomposition slows down (Hugelius *et al.* 2014). Half of the global below-ground organic carbon pool is stored in the tundra (Tarnocai *et al.* 2009). In the cool tundra ecosystems, thick layers of organic material build up onto the soils (Strahler and Strahler 2005). In turn, decaying may be impartial, and the partly decomposed plant material forms organic soil, such as peat (Figure 4). Peat is a porous soil type and it has a high water-retention capacity, due to its high organic content. Thus, changes in tundra vegetation and its decomposition process, and in turn, the tundra carbon budget may have drastic consequences to the global climate system (Myers-Smith *et al.* 2011).

Climate warming has increased the vegetation cover and biomass in the tundra, and this is referred to as greening (Forbes *et al.*

2010, Normand *et al.* 2013, Epstein *et al.* 2016, Keenan and Riley 2018). The greening tundra ecosystem is undergoing a major shift caused by the rapidly rising temperatures (Myers-Smith *et al.* 2015, Myers-Smith and Hik 2017). This may be reinforced by local factors, such as soil moisture (Weijers *et al.* 2018). Certain types of tundra vegetation, such as woody plants (dwarf shrubs and shrubs), are growing taller, increasing their coverage, and expanding their spatial distribution (Myers-Smith *et al.* 2011, Normand *et al.* 2013). This phenomenon is known as shrubification or shrub expansion, and it may have remarkable consequences beyond tundra regions as it feeds back to climate change through the interconnected cycles of water, energy, and carbon (Cahoon *et al.* 2012).

1.4 Plants

Water is a crucial resource for plants, yet, when scarce or excessive, it can lead to stress and disturbance (Giblin *et al.* 1991, Trahan and Schubert 2016). Plants use water in their physiological functions (Silvertown *et al.* 2015), such as nutrient uptake, photosynthesis, and reproduction (Rodríguez-Iturbe 2000, Kirkby 2016). Thus, water is the most important resource for vegetation and its establishment in many terrestrial biomes (Porporato and Rodríguez-Iturbe 2002). Soil moisture and other water aspects affect spatial patterns of vegetation, such as species occurrences, species richness, and community composition (le Roux *et al.* 2013, le Roux *et al.* 2014, Buri *et al.* 2020).

In addition to soil moisture, various indirect and direct factors affect plant growth, development, and geographical distribution (Mod *et al.* 2016). Geology, topography, macroclimate, and distance to the equator are indirect factors influencing direct factors, such as soils, water, temperature, wind, and solar radiation (Guisan and Zimmermann 2000). The direct factors

influence vital resources, such as soil and air moisture, nutrients, and photosynthetically active radiation (Whittaker 1965). These key factors for plant life, the resources and direct drivers, must be considered in ecological investigations (McGill *et al.* 2006, Austin and Van Niel 2011, Mod *et al.* 2016).

A topical approach for understanding the spatial distribution of plants is species distribution modelling (SDM). SDM is a framework for analysing the spatial or temporal patterns of species in relation to the environment (Guisan and Zimmermann 2000, Franklin 2010). This framework consists of three conceptual models: 1) an ecological model (such as the hypothesis, Table 1), 2) a data model (data structure, Table 2), and 3) a statistical model (model structure, Table 3) (Austin 2002). SDM is based on the spatial information on the occurrences of a given species and its key environmental predictors, and therefore, the predictors should represent a scale that is relevant for the ecology and physiology of the species (Austin and Van Niel 2011).

Plant communities and their relations to the environment can also be examined through plant functional traits (McGill *et al.* 2006). Traits provide a common currency for comparing ecosystems that have no species in common (Wright *et al.* 2004, Díaz *et al.* 2016). A functional trait is a direct measurement of plant properties related to the fitness of a plant and it reflects plant growth, survival, and reproduction (Violle *et al.* 2007). Plant size represents the net accumulated growth and loss processes and can be measured, for instance, as plant height. Plant structure can be represented, for example by leaf area, which controls the energy and water balance of a leaf (Díaz *et al.* 2016). Plant reproduction can be represented, for instance, by seed mass, which is related to the dispersal, seed bank persistence (e.g. frost-tolerance), germination timing, and establishment of a plant (Leiblein-Wild *et al.*

2014, Barak *et al.* 2018, Saatkamp *et al.* 2019). All in all, plant communities, their traits, and relationship to the environment influence multiple ecosystem processes and mechanisms related to soil water across biomes.

2 Materials and methods

I conducted these observational studies in mountain tundra at an ecologically relevant scale. This scale matches variation found in fine-scale soil moisture (**I**, **II**, **III** & **IV**) and other local factors, which have been shown to interact with tundra vegetation (**II** & **IV**). The study settings span over a large range found in these key factors (**I**, **II**, **III** & **IV**) and they cover a great number of tundra species (**II** & **IV**) and functional traits (**IV**), increasing the generalisability of the results (Franklin 1995, Austin 2002, McGill *et al.* 2006). In the ecological investigations (**II** & **IV**), I have used only main predictors and resource predictors for the given species or trait (Austin 1980).

Chiefly, I focused on a landscape between two massifs in sub-Arctic Fennoscandia (Table 2). In my analyses, I used data from extensive *in situ* moisture measurements from the top-soil layer (0 - 10 cm; **I**, **II**, **III** & **IV**) and intensive fine-scale vegetation surveys (1 m² plots; **II**, **III** & **IV**). Data for **I** and **III** were collected in the valley between Mount Saana and Mount Jehkas (69.05 N, 20.81 E), and for **II** on Mount Saana. In addition to Mount Saana, data for **IV** were collected in three other tundra sites located on both hemispheres: high-Arctic Svalbard (78.20 N, 15.73 E), low-Arctic western Greenland (66.95 N, -50.72 W), and sub-Antarctic Marion Island (-46.90 S, 37.73 E).

All data are based on 1 m² study plots. The study setting in **I** and **III** is based on 1043 plots in a systematically sampled grid (1.5 km x 2.0 km). In **I**, I used the full data set (n = 1043), whereas

in **III**, only a subset of the plots (171). In **II**, I had data from 21 study grids (8 m x 20 m), which were situated above the treeline (comprising of *Betula pubescens* ssp. *czerepanovii*). In **II**, I used a subset of 18 plots per grid, as the data on all three species groups (vascular plant, mosses, and lichens) were available only from this subset of plots (378). Whereas in **IV**, I used all 160 plots from each 21 grids in the sub-Arctic, in addition to the six high-Arctic grids, six low-Arctic grids, and nine sub-Antarctic grids.

Soil moisture was measured in volumetric water content (VWC%) using a hand-held time-domain reflectometry sensor. In **I**, the data were collected during the growing-season of 2016. In addition to soil moisture, I had data on the *in situ* measured depth of the soil organic layer. In **III**, the soil moisture measurements were carried out during the growing season of 2017, in addition to *in situ* measured soil temperature (snap-shot measurements), laboratory analysed data on soil organic carbon stocks, and field-quantified snow depth measurements. In **II**, I worked with three different water aspects: soil moisture level, temporal variation of soil moisture, and fluvial disturbance (*sensu* le Roux *et al.* 2013, le Roux *et al.* 2014). In addition, I had *in situ* data on soil temperature (miniature loggers), solar radiation (based on *in situ* slope and aspect measurements), soil pH (laboratory analyses from soil samples), geomorphological disturbances, and the coverage of the dominant allelopathic plant species (*Empetrum nigrum*) to account for biotic interactions (*sensu* Austin and Van Niel 2011, Mod *et al.* 2016). In **IV**, I used a harmonised dataset consisting of *in situ* soil moisture, soil temperature (miniature loggers), soil pH (laboratory analyses from soil samples), and solar radiation (based on *in situ* slope and aspect measurements) across all four study sites.

Articles **II**, **III**, and **IV** were based on

intensive vegetation surveys. In **III**, I used data on the coverage and height of woody plants as well as the overall coverage of vascular plants surveyed in 2016–2017. In **II** and **IV**, the species data from the sub-Arctic was collected in 2011–2013. In **II**, this data comprised the species occurrence and coverage percentage of vascular plants ($n = 116$), mosses (68), and lichens (87). In **IV**, I used only the species composition data of vascular plants, which had been collected from the high- and low-Arctic in the growing season of 2018, and from the sub-Antarctic in 2016–2017. In the high-Arctic there were 61 species, low-Arctic 75, sub-Arctic 134, and sub-Antarctic 18. Based on the species composition data, seven plant functional traits were derived from the Tundra Trait Team, TRY, and BIEN databases (Kattge *et al.* 2011, Bjorkman *et al.* 2018b, Maitner *et al.* 2018). This information was used to calculate community weighted means for seven functional traits, namely plant height, specific leaf area, seed mass, leaf dry mass content, leaf area, leaf nitrogen content, and leaf phosphorus content.

I collected the extensive field datasets together with the BioGeoClimate Modelling Lab (sub-Arctic site) and the le Roux Lab (sub-Antarctic site). In **I**, I measured a significant portion of the soil moisture and soil depth data in 2016. In **II**, I collected data on vascular plants and soil samples in 2013. In **III**, I collected most of the soil moisture data, and all the woody plant and snow data with my colleague Pekka Niittynen in 2017. In **IV**, I collected data on vascular plants and soil samples in the sub-Arctic site in 2013, and all the field data in the low-Arctic and high-Arctic sites with Pekka Niittynen in 2018. The data collected for this thesis are also used in other published articles (Happonen *et al.* 2019) and articles currently under review (Happonen *et al.*, Riihimäki *et al.*, Niittynen *et al.*).

I utilised topography-based variables derived

from high-resolution light detection and ranging (LiDAR) data provided by the National Land Survey of Finland (**I** & **III**). Based on the LiDAR data, a digital terrain surface model (1 m resolution) was calculated, from which elevation, potential solar radiation, topographic wetness index (TWI), and topographic position index (TPI) were calculated. In **I**, I also classified the surficial deposits of the study area using aerial imaging (0.5 m resolution; National Land Survey of Finland).

I analysed the data using several multivariate and correlative modelling methods (Table 3). In **I** and **II**, I used generalized linear models (GLM; Nelder and Wedderburn 1972), generalized additive models (GAM; Hastie and Tibshirani 1987), generalized boosted regression models (GBM; Elith *et al.* 2008, Greenwell *et al.* 2019), and random forests (RF; Breiman 2001) as I wanted to account for the uncertainties related

to each multivariate technique. I incorporated these four methods also in the SDMs (**II**). GLM and GAM represent regression models, whereas GBM and RF are regression tree models based on machine learning. These modelling methods are commonly used in ecosystem research and are suitable tools for investigating geographical and ecological phenomena.

In **III**, I used structural equation modelling (SEM). SEM is a theory-based hierarchical modelling technique, which enabled me to control for hierarchical position of other factors potentially influencing both vegetation and the soil conditions (Lefcheck 2016). SEM allows the simultaneous evaluation of several potential causal structures and I could model both direct and indirect effects. I assumed that various topographical factors would have an indirect effect on the soil and that vegetation would mediate this effect.

In **IV**, I used hierarchical generalized additive

Table 2. Data structures.

| Question | Article | Water data | Plant data | Study sites, plots | Soil moisture measurements |
|----------|------------|------------------------------------|--------------------------------------|--|--------------------------------|
| 1 | I | Spatial Temporal | - | Sub-Arctic, 1043 | 9387 |
| 2 | II | Spatial Temporal Disturbance | Vascular plants Mosses Lichens | Sub-Arctic, 378 | 3402 |
| | III | Spatial | Woody plants Vascular plants | Sub-Arctic, 171 | 2565 |
| 3 | IV | Spatial | Plant functional traits | High-Arctic, 960 Low-Arctic, 960 Sub-Arctic, 3360 Sub-Antarctic, 1440 | 2880 2880 30240 21600 |

models (HGAM), a conceptual extension of GAMs, to compare study sites across the hemispheres (Pedersen *et al.* 2018). I chose to use HGAM as the hierarchical approach enabled me to account for the structure of the study design and to compare if the four sites deviated from the global (all four sites) trait-environment relationship. In addition, HGAM can detect nonlinear functions of the predictor variables.








In addition, I analysed the data using ordination techniques (**II** & **IV**). The idea is to reduce dimensions in a multidimensional dataset, which may contain collinear variables, and to find the principal dimensions, according to which the data vary (Husson *et al.* 2017). By principal dimensions I mean, for instance, environmental variation (**II** & **IV**) and plant functional trait variation (**IV**). In **II**, I used non-metric multidimensional scaling (NMDS), which is a robust way to analyse unconstrained ordination in community ecology (Minchin 1987). In **IV**, I

performed principal component analyses (PCA).

3 Results and discussion

I found that in the tundra, topography and soil factors control the spatial variation of fine-scale soil moisture (< 10 cm), but not the temporal variation, which calls for more investigation (**I**). Water is strongly linked to local spatial vegetation patterns. Soil moisture and other water aspects influence species distribution, species richness, and community composition of vascular plants, mosses, and lichens (**II**). The relationships between environmental factors and plant functional traits are transferable between tundra sites (**IV**). I also found that while water is vital to plants, plants also influence soil moisture, as woody plants had a significant negative correlation with surface soil moisture (**III**).

Table 3. Model structures.

| Question | Article | Predictor | Mediator | Response | Method |
|----------|------------|--|---|---|---------------------------------|
| 1 | I | Topography Soil | - |  | GLM GAM GBM RF |
| 2 | II |  Resources Direct drivers | - |  | GLM GAM GBM RF NMDS |
| | III | Topography Snow |  |  | SEM |
| 3 | IV |  Resources Direct drivers | - |  | HGAM GAM PCA |

3.1 Soil moisture

To answer my first question “*What controls soil moisture variation?*”, I evaluated the physical conditions controlling soil moisture (I). I modelled the spatial variation of soil moisture using field-quantified information on the depth of the organic layer, aerial imaging-based surficial deposits classification, and LiDAR-based topography data. I used several statistical methods in the analyses, and the results indicated that the models performed similarly. On average, the model fit was reasonably good ($R^2 = 0.60$) as well as the predictive performance ($R^2 = 0.47$).

I found that fine-scale soil moisture shows great spatial variation over short distances. On average, soil moisture was 22.0 VWC%, ranging within the landscape from 4.6 to 78.2 VWC%. Both in varying terrains and flat landscapes, the fine-scale spatial distribution of soil moisture can be very heterogenous (Engstrom *et al.* 2005, le Roux *et al.* 2013). However, I found that topography and soils provide only little information on the proneness of the soil for temporal variation of moisture. Thus, this calls for re-evaluation of the conceptual model. In other words, the factors that control the spatial dimension of moisture are not the same for the temporal dimension, and therefore, it must be investigated with other types of data and from another perspective.

In the model, the spatial variation of soil moisture was most related to peat depth and the varying topography. Based on the relative importance of each variable, soil moisture related the most to the topography-based wetness proxy, TWI. This was also indicated by the relatively strong correlation between soil moisture and TWI (Spearman correlation 0.46). These results provide field-quantified evidence supporting previous studies (Isard 1986, Lookingbill and Urban 2004, Milledge *et al.* 2013).

The results are important as more high-

resolution terrain data is made openly available and used for creating moisture proxies (Jaboyedoff *et al.* 2012), which are widely used in microclimate and vegetation studies (Riihimäki *et al.* 2017, Greiser *et al.* 2018). These moisture proxies must be validated with field-quantified data to discuss how well they represent the spatial patterns of soil moisture. Overall, LiDAR has a huge potential in exploring moisture phenomena influenced by fine-scale terrain features (Lookingbill and Urban 2004, Famiglietti *et al.* 2008, Moeslund *et al.* 2019).

3.2 Plants

I approached my second question “*How is water linked to vegetation?*” from two perspectives: spatial vegetation patterns (II) and plant traits (IV). In II, I examined this from different aspects by quantifying three water variables (spatial and temporal variation of soil moisture and fluvial disturbance) and their influence on vascular plants, mosses, and lichens. More specifically, I explored the influence of these water aspects on the species distributions, species richness, and community composition of the three species groups.

In the model including all species groups, the inclusion of the water variables improved the predictive performance of the distribution models (area under the curve value from 0.73 to 0.75). When comparing the models of individual species groups, the increase was the highest in the species distribution models of mosses (from 0.69 to 0.73).

Of the three water aspects, the species distribution patterns were most related to the spatial variation of soil moisture. The species groups had diverse responses to soil moisture. Species distribution models of vascular plants responded positively or unimodally to moisture. Moss species had a strong positive response, whereas lichen species were most divided among

positive, negative, and unimodal responses. Species richness patterns of vascular plants and mosses showed similar patterns as in the distribution models, whereas lichen richness had an overall negative response to soil moisture.

The NMDS supported the results, as the community composition consisting of the three groups varied primarily according to fluvial disturbance and spatial variation of moisture among other important factors. The analysis also provided evidence for the independency of the distinct water aspects.

As climate change increases temperatures in tundra regions (Post *et al.* 2019), and in turn evaporation, the spatial distribution of vegetation is likely to become more reliant on water conditions (Crimmins *et al.* 2011, le Roux *et al.* 2013). Consequently, vascular plant, moss, and lichen communities will respond to the altered hydrological conditions (Iturrate-Garcia *et al.* 2016, Robinson *et al.* 2018, Kern *et al.* 2019). Soil moisture is important for tundra vegetation in multiple ways, and this is highlighted in its mediating potentials in the impacts of warming (Winkler *et al.* 2016, Nabe-Nielsen *et al.* 2017).

In IV, I explored soil moisture influencing plants by assessing if plant-environment relationships were generalisable in the tundra. The models explained 54% of the deviance in community weighted mean plant height, 60% in specific leaf area, 57% in seed mass, 80% in leaf dry matter content, 83% in leaf area, 64% in leaf nitrogen content, and 67% in leaf phosphorus content. Except for one, the plant-environment relationships were significant in all models ($p = 0.01$).

The local variation of environmental conditions within the four distinct sites was overridden by global relationships indicating that these links are generalizable. HGAM enables the analysis of whether the functional

relationship between the response and predictors had the same form for all four study sites and for them combined, in other words if generalisable relationships exist between the distinct plant communities and the environmental factors. The results provide empirical evidence for a cornerstone assumption in trait-based ecology: trait-environment relationships are transferable between plant communities (McGill *et al.* 2006, Shipley *et al.* 2016).

The results support studies based on macroclimatic water variables, qualitatively assessed soil moisture, and experimental studies, which have linked traits to plant-available water (Moles *et al.* 2009, Bjorkman *et al.* 2018a, Oddershede *et al.* 2018). Yet, there are only few field-quantified examples addressing this fundamental assumption on the generality and transferability of trait-environment relationships (McGill *et al.* 2006, Shipley *et al.* 2016).

In addition to soil moisture, the traits were most related to mean annual soil temperature. From a global change perspective, the results provide evidence to the expectation that tundra plants and their traits will respond to warming conditions (Bjorkman *et al.* 2018a). As temperatures will rise, plants will grow taller and have larger leaves with higher nutrient contents. If there are not enough water resources for plants to use, soil moisture may limit the growth of tundra plants. Overall, these shifts and their consequences are likely to feedback to the global climate system (Pearson *et al.* 2013).

3.3 Plants on soil moisture

In my third question “*Do plants influence water resources?*” I built upon the knowledge gained in answering the first question. I introduced plants into the equation to investigate if they had a direct impact on tundra soils, which mediated the influence of other factors (III). I approached the question from a hierarchical perspective using

SEM and constructing on the physical foundation (topography and snow) known to influence both tundra soils and vegetation. I found that the coverage of woody plants had a direct effect, as they inversely correlated with multiple soil properties.

While controlling other factors influencing both vegetation and soil properties, woody plant coverage correlated negatively with soil moisture, soil temperature, and soil organic carbon stocks (standardised coefficients = -0.16; -0.22; -0.27). None of the soil conditions were influenced by woody plant height. This indicates that as woody plants are expanding in the tundra, their effects on the soil conditions depend upon how the expansion occurs.

This fine-scale examination provides evidence supporting previous studies, which have found soil moisture to be lower in habitats with woody plants compared to other tundra habitats (Ge *et al.* 2017, Laffleur and Humphreys 2018), as well as studies, which have found that soil temperature is decreased by the overall shading of plants (Aalto *et al.* 2013, Myers-Smith and Hik 2013). Experimental studies suggest that the presence of shrubs also affect moisture retention negatively in reoccurring drought (Robinson *et al.* 2016).

Tundra plants influence the water (Bonfils *et al.* 2012), energy (Aalto *et al.* 2018), and carbon cycles (Cahoon *et al.* 2012). Yet, the impact on carbon stocks can be entirely context dependent, as currently there is no consensus on the impacts of woody plant on tundra carbon stocks. These results indicate that the presence of woody plants may decrease organic soil carbon stocks. This supports previous studies (Cahoon *et al.* 2012), but is also in contrast with others (Qian *et al.* 2010). Yet, the results are significant in the light that it is likely that expanding woody plants will feedback to the climate system in multiple ways through soils (Myers-Smith *et al.* 2011, Sørensen *et al.* 2018, Strimbeck *et al.* 2019).

3.4 Methodological issues

The results I found in **I**, **II**, **III**, and **IV** are based on correlative analysis of local observational data, which rises the issues regarding causality and scaling.

Firstly, without a solid conceptual model (Table 1), meaning the ecological theory and hypothesis, the interpretation of correlative results may lead to erroneous conclusions (Austin 2002). Yet, observational studies can be highly useful in ecosystem research and by using multivariate analysis it is possible to identify spatial patterns and influencing factors (Franklin 2010). Advanced tools enable the consideration of hierarchical structures within the data or environment (Lefcheck 2016, Pedersen *et al.* 2018). In **III**, SEM provided a valuable way to separate the direct and indirect effects of predictors and evaluate the mediating role of woody plants. In **IV**, I wanted to compare the study sites, but they shared no common species, which is why I used universal plant functional traits and the HGAM approach to assess whether the sites followed general patterns of plant-environment relationships.

Lastly, the spatial extent of the data can limit the generalisability of results. This I have addressed by utilising topographic complexity as an advantage (**I**, **II**, **III** & **IV**). Complexity increases patchiness of the landscape and controls the climatic range of the site (Graae *et al.* 2018). Consequently, a relatively concise spatial extent can contain broad gradients (such as soil moisture) covering a range of environmental conditions (Whittaker 1965, Billings 1973). Local variation can be overlooked by coarse-scale climatic data (Aalto *et al.* 2018), thus, fine-scale ecological studies should use relevant microclimatic data (Graae *et al.* 2012). Relevance depends also on the question, as variables can be presented in nearly limitless ways (Körner and Hiltbrunner 2018). Here, moisture is measured

from the surface soil (< 10 cm; **I, II, III & IV**), thus it does not represent the full soil layer or water reservoirs beneath it. Point measurements have a limited spatial and temporal extent (Figure 3). The first can be compensated by repeating the measurements over larger extents with dense spacing (Figure 2; **I, II, III & IV**). Yet, the temporal aspect of soil moisture can be truly captured only with continuous data (**I**). Luckily, new methods are developed and can be applied in future studies (Wild *et al.* 2019).

4 Future perspectives

Soil moisture has multiple effects on tundra plants (**II & IV**), and so do plants have on tundra soils (**III**). It is evident that climate change will affect the tundra ecosystems through the two-way link between plants and water. The next step is to address the chain of uncertainties between climate change, soil moisture, and tundra plants (Figure 6) (Porporato *et al.* 2004, Falloon *et al.* 2011, McLaughlin *et al.* 2017).

First, we must understand how climate change impacts are realised on the spatio-temporal patterns of fine-scale soil moisture (Bintanja and Andry 2017). As the climate is warming, the availability of soil water is likely to become globally threatened (Xu *et al.* 2013). Snow melt patterns have already shown evidence of change (Musselman *et al.* 2017, Niittynen *et al.* 2018). Snow melt timing influences temporal availability of soil moisture in the tundra (Blankinship *et al.* 2014), and is mediated by vegetation (Conner *et al.* 2016). Tundra ecosystems appear to be drying due to increased evaporation for the past decades in both the Arctic and the Antarctic. Ponds and lakes have dried (Smol and Douglas 2007, Nitze *et al.* 2017, Finger Higgins *et al.* 2019), and moss community composition and health as well as bird species richness have already declined

showing a strong negative responses to drying (Roach and Griffith 2015, Robinson *et al.* 2018). On the other hand, moisture released from thawing permafrost may temporarily increase the water content in surface soils (French 2007). As the climate change impacts will be uneven across the globe, the spatial distribution of soil moisture will be even more significant in the future (Jung *et al.* 2010).

Secondly, we need to find tools to accurately predict plant-available water at an ecologically relevant scale, especially from the temporal perspective (Nasta *et al.* 2018, Wild *et al.* 2019). The temporal variation of fine-scale soil moisture is controlled by other factors compared to its spatial variation (**I**). On coarse spatial scales, there are tools to investigate soil moisture globally (McColl *et al.* 2017) and regionally (Blyverket *et al.* 2019), and long-term records (> 40 years) are also available (Gruber *et al.* 2019). Yet, in order to understand soil moisture and its future, we need fine-scale predictions on factors influencing the temporal variation of soil moisture (Fatichi *et al.* 2020), such as precipitation (Bintanja and Andry 2017), evaporation (Mastrotheodoros *et al.* 2020), and snowmelt (Niittynen *et al.* 2018), which are highly impacted by increasing temperatures of the high-latitudes and high-altitudes. Most of all, we need tools for transforming this information into temporal predictions of fine-scale soil moisture over large regions (Blyverket *et al.* 2019, Fatichi *et al.* 2020). It is challenging to predict the influence of climate change on plant-available water, as the prevailing microclimate does not directly reflect on soil moisture conditions (Brocca *et al.* 2012), and can be remarkably decoupled from the macroclimate (Aalto *et al.* 2018).

Thirdly, plant-water relationships cannot be explored without acknowledging the significant impacts that plants have on soil moisture (**III**)

(Aalto *et al.* 2018, Mastrotheodoros *et al.* 2020). It is important to analyse the mechanisms of how the on-going tundra vegetation changes will affect soil water conditions (Robinson *et al.* 2019). Here, global databases can help as they provide useful snapshots of biodiversity (IV), yet so far only a fraction of all plants have been thoroughly documented and openly shared with the research community (Cornwell *et al.* 2019). More field data, climate change research, and standardised protocols are urgently needed

(Halbritter *et al.* 2019, Lembrechts and Lenoir 2019), especially when it comes to less studied organisms, which yet are a significant part of the tundra (Roos *et al.* 2019). For instance, mosses, lichens, and microalgae are abundant and ecologically important producers and regulators in the tundra (Sommerkorn *et al.* 1999, Uchida *et al.* 2006, Blok *et al.* 2011, Pushkareva *et al.* 2016). Thus, not only vascular plants, but all the cornerstone species groups must be studied in relation to water resources and climate change,

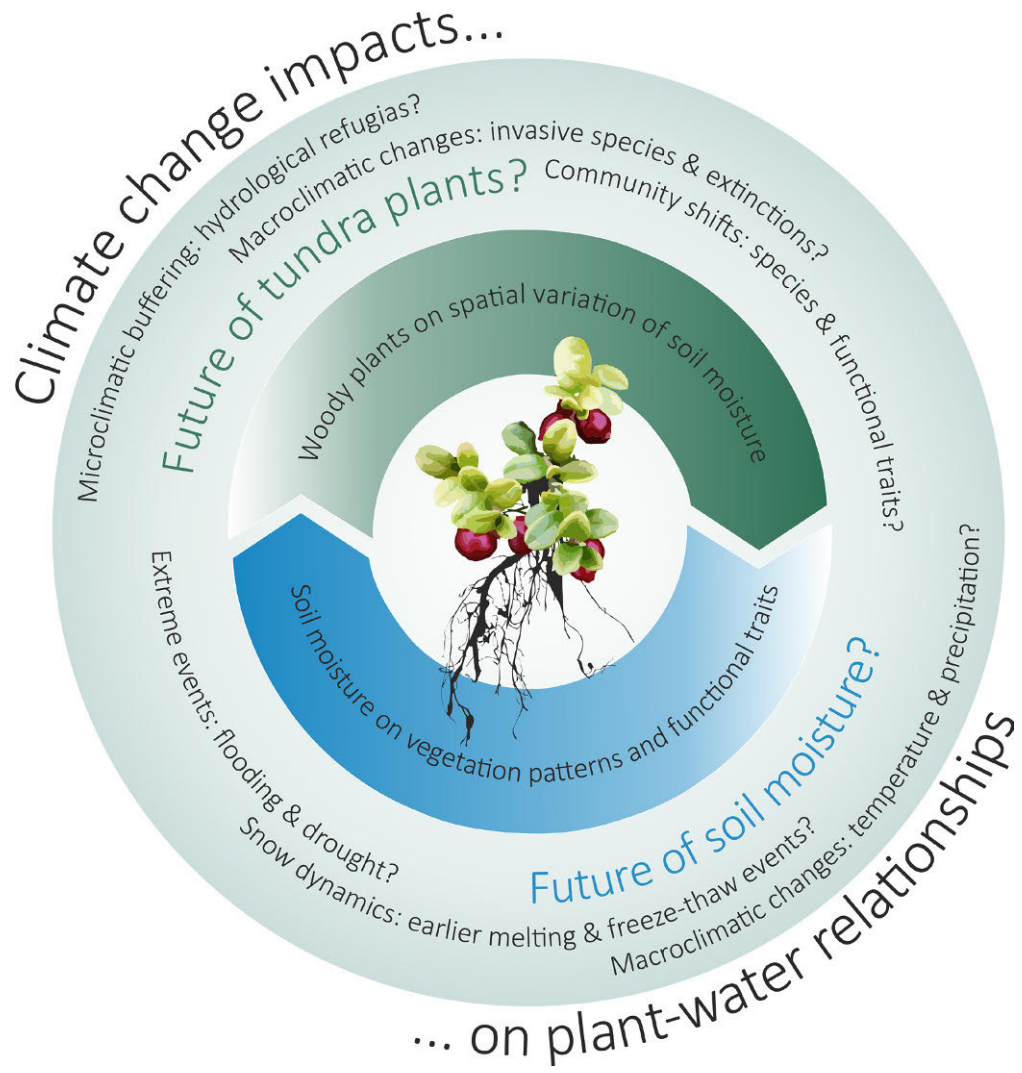


Figure 6. Future perspectives. Climate change impacts may drastically affect fine-scale plant-water relationships, which may, in turn, feedback to global climate change through the effects of water conditions on plants as well as the effects of plants on soil water.

if we want to comprehensively understand the ecosystem functions and processes in future (II).

Finally, climate change impacts on the water cycle are likely to affect all life on Earth, from humans to microbes (Barnett *et al.* 2005, McCalley *et al.* 2014, Classen *et al.* 2015, Hansen *et al.* 2016), and from the tropical rainforests to the polar deserts (Engelbrecht *et al.* 2007, Robinson *et al.* 2018). Complex topography increases small-scale heterogeneity in water and energy conditions (Graae *et al.* 2018, Hoylman *et al.* 2018). This is reflected on vegetation, as the sensitivity of the ecosystem decreases and its climate change buffering capacity increases along varying moisture conditions (Alatalo *et al.* 2017, Buri *et al.* 2020). Soil moisture mediates rising temperatures (Crimmins *et al.* 2011, Ashcroft and Gollan 2013, Winkler *et al.* 2016), which creates humid and cool microclimatic pockets increasing the overall ecosystem resilience (Holec and Wild 2011). Overall, the expected changes in the hydrological cycle and their consequences are not limited to a single species, ecosystem, or biome (Knapp *et al.* 2008). Thus, the exploration of soil moisture and its importance for all life must go on.

5 Conclusions

Soil moisture varies remarkably over short distances in rugged landscapes. This fine-scale variation provides a range of distinct habitats and increases biodiversity and decreases sensitivity of tundra ecosystems. Influenced both by the abiotic and biotic environment, soil water conditions affect vegetation across species and functional traits, from individuals to plant communities.

It is important to acknowledge that moisture and factors influencing it are highly scale dependent, and macroclimatic data may not provide the necessary information at a meaningful

scale. Thus, I highly encourage the use of field-quantified measurements when exploring fine-scale plant-environment patterns, whether they be species assemblages or functional traits.

Climate change is rapidly impacting the tundra ecosystems in the Arctic, Antarctic, and alpine regions, and part of this is due to the impacts on soil moisture. Here, the importance of soil moisture is unravelled regarding the vulnerable tundra ecosystem. Thus, it is crucial to carefully consider plant-water relationships in future studies.

In this thesis, I have highlighted the variability of fine-scale soil moisture and its importance for high-latitude vegetation. Yet, I have barely scratched the (soil) surface. The next step is to expand this knowledge beyond tundra and plant communities.

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Plant-water relationships are strong across the tundra. Soil moisture and its spatial variation are controlled by the soil characteristics and topographic features in the landscape, but also by the abundance of woody plants. Water conditions affect vegetation across species groups, from individuals to the communities. This knowledge unravels the importance of soil moisture in a vulnerable ecosystem undergoing rapid changes.

I am a soil moisture enthusiast to the core and a plant lover at heart. In my PhD, I first modelled soil moisture, then analysed plant-water relationships and finally used plants to model soil moisture. Now me, soil moisture and the tiny tundra plants have come full circle in this exciting Arctic adventure.

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